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PANTHERA ATROX (MAMMALIA: FELIDAE) FROM CENTRAL ALASKA

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ABSTRACT—A lower jaw of the large Pleistocene cat *Panthera atrox* (Leidy) was found on an alluvial flat about 180 miles northeast of Fairbanks, Alaska. It was probably washed out of carbonaceous silt deposits which, in the adjacent area, have also yielded bones of *Equus*, *Bison*, *Rangifer*, *Cervus*, and Elephantidae. The *Panthera* jaw falls within the size range of the series from Rancho La Brea, California, and differs from Rancho La Brea specimens only in a few characteristics. *P. atrox* appears to have been significantly larger than extinct or modern Asian tigers. Despite continuity of the American and Asian land masses at times during the late Pleistocene, present evidence indicates discontinuity between the populations of great cats on the two continents.

INTRODUCTION

A RIGHT lower jaw of the large Pleistocene cat, *Panthera atrox* (Leidy) (U. S. National Museum 23619) was found on an alluvial flat near the mouth of Lost Chicken Creek, Alaska, in September 1964, by Terry Clark and Helen L. Foster, U. S. Geological Survey. The find was made during the course of geological and terrain mapping of the Yukon-Tanana Upland.

Lost Chicken Creek is a very small, short (6,300 feet long) stream in east-central Alaska; it flows south and southeast into the South Fork of the Forty Mile River in T. 26 N., R. 18 E., Eagle A-2 quadrangle, U. S. Geological Survey 1:63,360 Topographic Map Series. The Taylor Highway crosses Lost Chicken Creek near milepost 69, about 180 miles northeast of Fairbanks.

Gold was discovered near the head of Lost Chicken Creek in 1901 (Prindle, 1905, p. 48), following earlier discoveries in nearby Chicken Creek. Gold-mining operations along Lost Chicken Creek, which have continued intermittently to the present, have removed considerable terrace material, and in the process mammal bones have been washed out. Local bone collectors regularly search the debris along Lost Chicken Creek just below the mining operations.

The unconsolidated Pleistocene deposits near the head of Lost Chicken Creek are believed to rest on Tertiary subaerially deposited sedimentary rocks, which include sandstone, shale, and coal. Plant remains and impressions have been found in these sedimentary rocks (Prindle, 1905, p. 48). However, most of the Pleistocene deposits of Lost Chicken Creek rest on a weathered surface of porphyritic quartz diorite (Prindle, 1905, p. 47, 48). The general section of the Pleistocene deposits along Lost Chicken Creek consists of up to 75 feet of rounded, locally loosely cemented and limonitic-stained stream gravel.

Only a few feet of the gravel is exposed along the stream but it has been encountered in deep holes. The gravel is generally overlain by brown sand and sandy gravel up to 10 feet thick; the sand and gravel are in turn overlain by 20 or more feet of stony silt. Locally the sand layer may be thin or absent so that the silt directly overlies the gravel. Carbonaceous layers are present in the silt. Peat deposits up to 15 feet thick overlie the silt in places. The peat and silt are generally permanently frozen at depths 2 or 3 feet below the surface.

The bone does not show wear from being transported; it is therefore conjectured that the mandible of *Panthera atrox* washed out of carbonaceous silt deposits exposed near the mouth of Lost Chicken Creek not far from where the bone was found. The following bones, now in the collection of the U. S. National Museum, were found in the valleys of Lost Chicken Creek and adjacent Chicken Creek, derived from deposits of the same type that yielded the jaw of *P. atrox*.

Perissodactyla

Equus sp. cf. *E. niobrarensis alaskae* Hay: partial mandible, with right I₁, I₃, C, and P₂ and left I_{2,3} and C (USNM 23620); and an upper molar (USNM 23621).

Equus sp.: radius of a small horse (USNM 23622); metacarpal of a slim, long-legged horse (USNM 23623); metatarsal and humerus of a small horse (USNM 23624 and 23625).

Artiodactyla

Bison bison (Linnaeus): M₃ and two upper molars (USNM 23626).

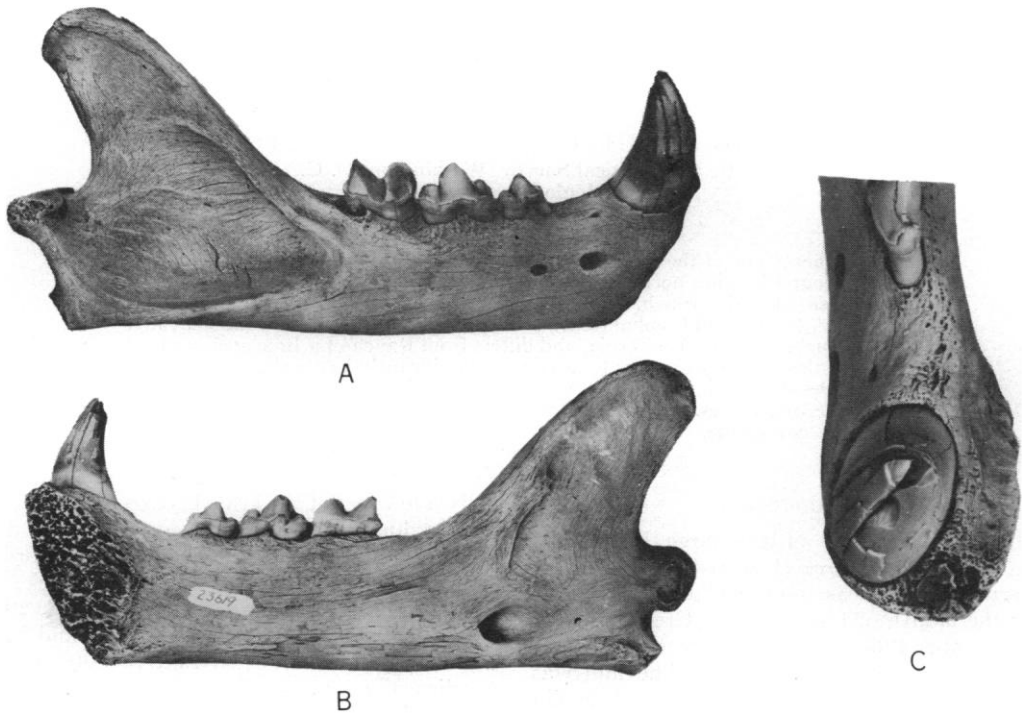
Bison sp.: metacarpal, somewhat larger than the modern species (USNM 23627).

Rangifer arcticus Richardson: right lower jaw (USNM 23628).

Rangifer sp.: metacarpal (USNM 23629).

Cervus sp.: antler fragment from a large individual (USNM 23630).

Another horse radius (USNM 23633) was



TEXT-FIG. 1.—Right lower jaw of *Panthera atrox*, USNM 23619. A, lateral view, $\times \frac{1}{4}$; B, medial view, $\times \frac{1}{4}$; C, dorsal view of symphyseal region showing atrophied incisors, canine, and anterior half of P_3 , $\times \frac{2}{3}$.

found in the bed of Lost Chicken Creek near the mouth of the stream. The radius is less weathered than the other bones and may come from a Recent horse. In addition to the above specimens, an I_3 and several terminal phalanges of *Equus* are in the collection of Mrs. Ann Purdy of Chicken, Alaska. Bones and teeth of Elephantidae are also commonly found by local collectors and miners along Chicken Creek.

SYSTEMATIC DESCRIPTION

Class MAMMALIA

Order CARVIVORA

Family FELIDAE

PANTHERA ATROX (Leidy) 1953

Text-fig. 1

The reader is referred to Merriam & Stock (1932), especially plates 32 and 33, for figures, measurements, and descriptions of the only large population sample of *Panthera atrox* (that from Rancho La Brea, California) that has been described.

USNM 23169: Right mandibular ramus of an old individual, larger than the mean of measurements of 16 individuals listed by Merriam & Stock (1932, table 92) but smaller than the type of the species (No. 12546, Academy of Natural Sciences, Philadelphia). Angle between symphy-

sis and inferior edge of ramus 125° ; chin sharply marked. No inferior symphyseal tubercle. Symphysis open. Dorsal surface of ramus in diastema rounded rather than sharply ridged. Inferior border of ramus convex; widely extended below masseteric fossa, which is deep and extends anteriorly to a point below posterior end of M_1 . Ventral outline of horizontal ramus about midway between extremes of convexity and concavity seen in Rancho La Brea population (Merriam & Stock, 1932, fig. 142). Angular process broken. Articular process smoothly curved dorso-ventrally; heavier than in either lion or tiger; resembles that of lion or jaguar more than tiger. Coronoid process does not project backward beyond posterior end of condyle; in this it differs from 16 of the 17 Rancho La Brea specimens examined by Merriam and Stock. Of Recent tiger jaws in the U. S. National Museum, the two from Korea (*P. tigris longipilis*) had coronoid processes extending back of the condyle. Of 10 Indian tigers, 2 had a backward-extending coronoid and 8 did not. Two vascular foramina, a millimeter apart and each about 2 mm in diameter, lie 17 mm below medial side of canine. Two mental foramina, 12.5 mm apart: anterior, 5.3 mm in diameter, lies below middle of diastema; posterior, 5.6 mm long by 3 mm high, lies below

anterior half of P_3 . Only two incisors present: median one represented by alveolus only, which shows the tooth to have been reduced and laterally compressed; lateral one occupied by a laterally compressed tooth that appears to have been pathologically eroded in life and to have been nonfunctional. Compression and reduction of incisors is probably a function of advanced age. Canine large, with marked wear facet on posterolateral side. P_3 two-rooted: distinct but small anterior cusp; principal cusp slightly higher than long, with apex slightly posterior to middle of cusp; posterior cusp larger than anterior cusp, and separated from principal cusp by shallow groove. P_4 : anterior cusp rounded, separated from principal cusp by deep notch; principal cusp higher than long, apex median, anterior slope of cusp longer than posterior slope. Both anterior and posterior sides of principal cusp of P_4 are vertical near base; posterior vertical face about twice as high as anterior one. As this is an old individual and these vertical faces have not disappeared with wear, they can be assumed to be present throughout the adult life of the animal. A P_4 of *Panthera atrox* from Rancho La Brea figured by Merriam & Stock (1932, pl. 33, fig. 7a) exhibits a smaller posterior vertical face on the principal cusp and no anterior vertical face (*i.e.*, the anterior slope of the principal cusp is uninterrupted until it meets the notch separating principal cusp from anterior cusp). Among living great cats, the configuration of the principal cusp of P_4 in the Alaskan *P. atrox* is most nearly reproduced in the lion (cf. Kabitzsch, 1960, fig. 4). Posterior cusp rounded, larger than anterior cusp but of same height; separated from principal cusp by deep notch; bordered posterolingually by a cingulum. M_1 : relative dimensions of paraconid and protoconid obscured by extreme wear; talonid conspicuous as in tooth figured by Merriam & Stock (1932, pl. 33, fig. 6,6a) and more conspicuous than in lion, tiger, jaguar, or leopard (Kabitzsch, 1960, p. 110).

DISCUSSION

Frick (1930) reported the presence of *Panthera atrox* in frozen muck near Fairbanks, Alaska. He named, without describing, a new subspecies, *Felis atrox alaskensis*. The name is thus a *nomen nudum* (Simpson, 1941, p. 23). Decision as to whether such a subspecies exists must await study of a series of specimens from Alaska. The single jaw from Lost Chicken Creek falls within the size range of the series from Rancho La Brea, California (table 1). It differs from the majority of Rancho La Brea specimens only in a few characteristics: the coronoid process does not extend posterior to the condylar process; the diastema is

relatively short; the symphyseal angle is more acute, and hence the front of the jaw presents a more nearly square profile than do the specimens figured by Merriam & Stock (1932, pl. 32).

The geographic range of *Panthera atrox* extends from Alaska to the Valley of Mexico (Freudenberg, 1910) and from California to Florida (Kurtén, 1965). Before Kurtén reported the species from Florida, it had not been definitely identified east of Natchez, Mississippi, where the type specimen was found (Leidy, 1853). Also present in eastern North America in Pleistocene time was the large jaguar called *Panthera onca augusta* by Simpson (1941). This subspecies has not been well identified west of Nebraska. The overlap of ranges of *P. atrox* and *P. onca augusta* may be explained by a difference in habitat. Kurtén (1965, p. 223) states that, whereas the jaguar is mainly a forest animal, *Panthera atrox* appears in association with plains animals at Rancho La Brea. Preference of *P. atrox* for open country is perhaps consonant with its presence in Arctic tundra.

West of the range of *Panthera atrox* is the range of the great cats of Manchuria, Korea, and north China—Pleistocene and Recent tigers and fossil cats of doubtful specific affinity. The areas of these two adjoining ranges were continuous at least twice during Wisconsin time, once more than 35,000 years ago and once between 25,000 and 12,000 years ago (Hopkins, 1959, p. 1525). During the first of these periods of emergence, which coincided with the most intensely glaciated phase of early Wisconsin time, a land area more than 1000 miles in north-south width connected Siberia and Alaska. This area was glacier free and thus available to migrating animals. In the opinion of Hopkins (1959, p. 1526), this land bridge never supported forests during Pleistocene time; a severe Arctic climate probably prevailed there during the Wisconsin glacial interval and also in earlier Pleistocene time. American immigrant mammal genera having an earliest known record in Wisconsin time are predominantly those characteristic or tolerant of Arctic-alpine environments (Hibbard *et al.*, 1965, p. 517).

At its maximum width, the Bering land area was so wide that the unglaciated part of Alaska was continuous with northeast Siberia, rather than a separate area connected by an isthmus (Hopkins, 1959, fig. 5D). The presence of large herbivores in this region (Elephantidae, Bovidae, Equidae) indicates a faunal situation favorable for large carnivores. This raises the question whether there might have been continuity (or at least ancestor-descendant relationships) of the large-carnivore population across the tundra of the Bering land bridge similar to that of the

TABLE 1.—Measurements (mm) of mandibles of *PANTHERA ATROX* and *PANTHERA TIGRIS*

	<i>P. atrox</i> USNM 23619	<i>P. atrox</i> , Rancho La Brea. Range of measurements (N = 16) ¹	<i>P. tigris</i> <i>longipilis</i> , Korea. USNM (N = 2) (Recent)	Vladi- vostok tiger (Recent) ²	Man- churian tiger (Recent) ³	Indian tiger USNM (N = 10) (Recent)
Length, anterior end of symphysis to posterior side of condyles	255.0	206.0–318.0	210.0	218.0	223.0	191.0–214.0
Length of symphysis	73.0	67.2–99.3	62.5–65.3	—	82.0	59.5–75.0
Depth of ramus below anterior end of P ₄	50.0	38.9–60.7	32.0–35.3	—	—	32.0–39.6
Depth of ramus below posterior end of M ₁	54.0	46.0–67.1	42.5	—	—	38.0–46.4
Thickness of ramus below posterior end of M ₁	20.6	20.0–36.9	21.0	—	—	15.5–23.0
Height from inferior border of angle to summit of condyle	54.2	42.0–66.4	40.0	—	—	37.5–53.6
Height from inferior border of angle to summit of coronoid process	125.0	96.3–150.0	92.3	—	111.0	84.0–118.0
Transverse width of condyle	51.9	44.5–74.9	53.0	—	57.0	43.5–57.0
Greatest depth of condyle	22.3	18.4–27.2	14.2	—	—	12.3–18.0
Canine, antero-posterior	30.0	21.8–30.4	21.4–23.3	25.0	28.0	20.7–28.0
Canine width	21.5	15.1–21.6	14.3–16.5	15.7	17.5	11.4–20.0
Length, front of canine to back of M ₁	132.0	116.4–156.7	100.0–114.0	—	—	100.4–115.0
Length, front of P ₃ to back of M ₁	75.0	68.3–89.0	57.0–63.0	—	—	57.7–68.0
P ₃ length	18.4	17.0–21.6	14.0–15.5	15.9	16.5	13.5–19.3
P ₃ width	9.5	9.4–13.2	7.4–8.0	8.9	8.5	7.0–8.4
P ₄ length	27.8	25.8–32.3	20.6–22.5	22.8	24.0	21.4–25.0
P ₄ width	13.0	12.6–16.9	10.4–10.4	10.0	11.5	10.0–12.0
M ₁ length	27.3	26.9–33.9	21.3–24.3	24.5	27.0	22.4–28.0
M ₁ width	13.5	13.0–17.5	11.0–11.4	12.2	12.5	11.0–13.4

¹ From Merriam & Stock, 1932, tables 92 and 94.² From Hooijer, 1947, table 3.³ From Busk, 1874.

Elephantidae and Bovidae. *Panthera atrox* was the large feline predator of the Alaskan late Pleistocene fauna; its occurrence in central Alaska, an area of continental climate, indicates probable cold tolerance. In the modern fauna of Asia, some degree of cold tolerance is shown by the present occurrence of tigers as far north as Irkutsk, at 53° north latitude (Hesse, Allee & Schmidt, 1951, p. 18). Pocock (1929, p. 509) states that the tiger survives in Mongolia, Amurland, Manchuria, and Korea. Large Pleistocene cats ranged far north of this, to the Yana River in northern Siberia (70°–72° N. lat.) and to the New Siberian Islands (75°–77° N. lat.), where Tscherski (1892) reported them in association with, among other species, *Oribos moschatus*, *Bison priscus*, *Ovis nivicola*, *Alces palmatus*, *Rangifer tarandus*, *Cervus canadensis* var. *maral*, *Rhinoceros tichorhinus* and *Elephas primigenius*. The felid material studied by Tscherski consisted of a femur, two astragali, a metatarsal, and a phalanx. These were identified as belong-

ing to *Felis tigris*. Identification as modern great cat can be accepted on the basis of the height of the greater trochanter of the femur, which rises slightly above the level of the femoral head (Tscherski, 1892, pl. 1), as contrasted with the femur of *Panthera atrox* in which the greater trochanter is distinctly lower (Merriam & Stock, 1932, pl. 38).

Merriam & Stock compared *P. atrox* with the great cats of the Old and New World. They noted resemblances of *P. atrox* with both lion and tiger but, as Simpson (1941) emphasized, found its closest modern counterpart in *Panthera onca*. In comparing *P. atrox* with the great cats of Asia, they found that "not only is there close correspondence in size, but there is likewise considerable resemblance in structural details" between *P. atrox* and *Felis spelaea* of the Old World Pleistocene (Merriam & Stock, 1932, p. 190, table 95). The ranges of these two species are separated by almost the whole of Asia, in which there have been found only a few Pleistocene cats of com-

parable size. Pei (1934, p. 135) calls attention to "a very striking analogy of size and shape" between *Panthera atrox* and his *Felis youngi* from locality 1 of Choukoutien. *Panthera* cf. *tigris* from Choukoutien (Pei, 1934, p. 132) is about intermediate in size between *P. atrox* and Recent *P. tigris*, as also is *Panthera tigris* subspecies from the Pleistocene of Wanhhsien, China (Hooijer, 1947, table 2). On the other hand, modern Asiatic tigers are consistently smaller than *P. atrox* (table 1); this is true even of the few northeast Asian tigers for which measurements are available. Hooijer (1947, p. 12) states that the Siberian tiger has decreased little, if any, in size since the Pleistocene, a fact which suggests a difference in size range between Pleistocene Asiatic tigers and *P. atrox*.

CONCLUSION

Despite continuity of the American and Asian land masses at times during the late Pleistocene, present evidence indicates discontinuity between the populations of great cats on the two continents.

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